

TRANSPIRATION DURING LIFE CYCLE IN CONTROLLED WHEAT GROWTH

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ABSTRACT

We use a previously-developed model of wheat growth, which was designed for convenient incorporation into system-level models of advanced space life support systems. We apply the model to data from an experiment that grew wheat under controlled conditions and measured fresh biomass and cumulated transpiration as a function of time. We examine the adequacy of modeling the transpiration as proportional to the inedible biomass and an age factor, which varies during the life cycle. Results indicate that during the main phase of vegetative growth in the first half of the life cycle, the rate of transpiration per unit mass of inedible biomass is more than double the rate during the phase of grain development and maturation during latter half of the life cycle.

THE GROWTH MODEL

We developed a model for the growth of wheat /1/, which proved useful for coupling the wheat with other components in a system-level model of a Controlled Ecological Life Support System (CELSS). The rationale for the model's form is that growth curves of most crops prominently show the S-shaped or sigmoidal curve typical of biological systems. The solution to the logistic differential equation imitates this S-shape of exponential growth followed by a leveling-off. In the logistic equation, $dM/dt = rM(1-M/K)$, where M is the biomass and t is time, there are two parameters: r and K . The r is the growth rate for the purely exponential part of the system. K , the carrying-capacity in an ecological system, in this case is the maximum biomass reached by the crop. The logistic equation thus contains some biologically meaningful parameters.

While the logistic equation can be applied directly to the growth of the inedible biomass of a crop, the equation for the edible crop parts is here somewhat differently structured (see also /2,3/). Like the inedible cells, the edible cells reproduce and the total edible growth must be proportional to the edible mass (M_{ed}). However, the edible parts do not produce their growing mass through photosynthesis, but rather receive photosynthetic products from the inedible parts (in particular, the leaves); therefore, the inedible biomass (M_{ined}) should also appear in the edible equation. Furthermore, since the edible growth occurs substantially after the beginning of the inedible growth (about halfway through the life cycle for wheat), a time that initiates the growth of the edible mass (t^*) is incorporated into the edible equation. Before t^* the edible biomass is assumed equal to zero, and its growth is initiated at t^* with a minimum edible mass (E_{min}). The full set of equations is (see also /2,3/):

$$\frac{dM_{ined}}{dt} = r_{ined} M_{ined} \left(1 - \frac{M_{ined}}{K_{ined}}\right) \quad (1)$$

$$t < t^* : \quad \frac{dM_{ed}}{dt} = 0 \quad (2a)$$

$$t > t^* : \quad \frac{dM_{ed}}{dt} = r_{ed} M_{ined} \left(\frac{E_{min} + M_{ed}}{K_{ed}}\right) \left(1 - \frac{M_{ed}}{K_{ed}}\right) \quad (2b)$$

The parameters t and t^* are in units of time, r_{ined} and r_{ed} are in units of time^{-1} , and all other parameters (M_{ed} , M_{ined} , K_{ed} , K_{ined} , E_{min}) are in identical units of either dry mass or dry mass per unit area. The system of equations (1a-c) above was used for wheat, soybean, and potato /2/. The total fresh biomass (B) is the sum of the fresh edible and inedible masses, expressed using their respective ratios (w_i 's) of their wet (fresh) mass to dry mass:

$$B = w_{ed} M_{ed} + w_{ined} M_{ined} \quad (3)$$

We compare the model to data provided by S. Schwartzkopf /4/. He grew wheat at the NASA Ames Research Center under controlled conditions of temperature, humidity, and atmospheric CO₂ (1200 ppm). Since we are not concerned here with how growth is affected by changes in these variables (except for humidity, see below), or other parameters (such as planting density), this data has been normalized to the total fresh biomass at day 60 (B_{60}), which in his experiment was the maximum total fresh biomass reached during the seed maturation. Figure 1a plots this normalized value of B/B_{60} as a function of time for the wheat data.

Equations (1, 2a-b, and 3) are run with $w_{ed} = 1.13$ (gm fresh per gm dry) /5/ and $w_{ined} = 5.7$ (gm fresh per gm dry) /6/. Other parameters used here are $K_{ed} = 2500$, $K_{ined} = 3700$, $E_{min} = 80$, initial $M_{ined} = 10$. In previous models these units have been gm dry mass m^{-2} , but here the units may be considered arbitrary since to facilitate comparison to Schwartzkopf's data, the model's output is normalized as a ratio between total fresh biomass and the total fresh biomass at day 60. This ratio, B/B_{60} , is plotted in figure 1a. Note also that the harvest index, defined as the fraction of the edible dry biomass—here approximately $2500/(2500+3700)$ —is consistent with the value of 0.4 from data /5/. The only major unknowns that can influence the shape of the growth curve significantly are the growth rates; these are adjusted to produce a reasonably accurate fit to data. The model curve shown in figure 1a uses $r_{ed} = r_{ined} = 0.2 \text{ day}^{-1}$.

TRANSPIRATION FORMULATION

Transpiration will probably account for about half the energy balance in the plant growth system of a CELSS. By definition, the total transpiration rate (Γ) is proportional to the transpiration rate per unit of inedible biomass (γ) and to the total inedible biomass. Therefore

$$\Gamma = \gamma M_{ined} \quad (4)$$

Following general reasoning such as that given in Gates /7/, γ is a function of the difference between the partial pressures of water vapor in the leaf ($P_{H_2O,leaf}$) and atmosphere ($P_{H_2O,air}$) and a function of the stomatal resistance (f_s), which itself a complex function of various environmental factors including light, temperature, and CO₂.

$$\gamma = \gamma^* f_h f_s f_a \quad (5)$$

Here we have written γ as a product of a humidity factor (f_h is a function of $P_{H_2O,leaf} - P_{H_2O,air}$), a stomatal resistance factor (f_s), a unit normalizing constant γ^* , and an age factor (f_a), which accounts for changes in the plant's transpiration rate per unit inedible biomass during its life cycle even when all environmental factors (f_h, f_s) are constant. A $\gamma = \text{constant} = 2.4 \text{ gm H}_2\text{O per gm dry inedible biomass per day}$ (this gives a rough average of typical wheat under controlled environments /8/) was used by Rummel and Volk /1/, but could not be tested against data during the plant's life cycle at that time. S. Schwartzkopf has been able to take detailed transpiration data from wheat /4/. To facilitate comparison between model and data the cumulated transpired water at time t ($\int_0^t \Gamma dr$) is normalized to the cumulated transpired water at day 60 ($\int_0^{60} \Gamma dr$). This ratio— $\int_0^t \Gamma dr / (\int_0^{60} \Gamma dr)$ —is plotted as a function of time in figure 1b. It is also useful to consider the instantaneous transpiration rate Γ (here calculated from the data on cumulated water for any point using the previous and subsequent points), also normalized to the cumulated transpired water at day 60. This ratio— $\Gamma / (\int_0^{60} \Gamma dr)$ —has the units of day^{-1} , and should be read as the fraction of the total transpired water during the life cycle transpired during a given day; this ratio is plotted in figure 1c.

$$\text{Normalized cumulated transpiration} = \frac{\int_0^t \Gamma dr}{\int_0^{60} \Gamma dr} \quad (6a)$$

$$\text{Normalized transpiration rate} = \frac{\Gamma}{\int_0^{60} \Gamma dr} \quad (6b)$$

Schwartzkopf's humidity controls kept the relative humidity (rh) at 0.35 at the beginning of the experiment, but only maintained rh near 0.45 at the end /4/; the change was gradual and approximately linear. Assuming leaf rh = 1.0 and air rh varied from 0.35 to 0.45, the humidity factor f_h , expressed in terms of rh and non-dimensionalized to the final condition, is taken here to have varied linearly from 1.18 at the beginning of the experiment $((1-0.35)/(1-0.45))$ to 1.00 at the end. Furthermore, we set $\gamma^* = 2.4 \text{ gm H}_2\text{O per gm dry inedible biomass per day}$, and since environmental conditions were approximately constant, $f_s = 1.0$ for the duration of the experiment. We test several cases of the age factor f_a .

The first case has $f_a = 1.0 = \text{constant}$ (or, $\alpha = 0$, see below). Output from the model for cumulated transpiration and transpiration rate is normalized to the cumulated transpiration at day 60 using equations 6a-b, like the experimental data. Note this normalization effectively eliminates dependence of the results on γ^* . Results with f_a

= constant are plotted against data in figures 1b and 1c. Although the general shape of the cumulated transpiration data is matched by the model (see figure 1b), the empirical value is significantly underestimated during the middle one-third of the life cycle. The underestimation is even clearer in the rate results, shown in figure 1c. For the first one-half of the life cycle, the transpiration rate in the model is much too low.

A second case explores the possibility that the transpiration rate per unit inedible biomass is substantially higher when the plant is younger than when mature. A convenient way of parameterizing this process that takes into account the apparent steadiness of the transpiration rate during the second one-half of the life cycle, when the inedible biomass itself is relatively maximum and constant, is to write f_a as a function of M_{ined} :

$$f_a = 1 + \alpha \left(1 - \frac{M_{ined}}{K_{ined}} \right) \quad (7)$$

Here the term α is an enhancement of transpiration rate per unit biomass when the plant is young. Note $f_a = 1.0$ when $M_{ined} = K_{ined}$. The model output for cumulated transpiration and transpiration rate for this second model—which uses $\alpha = 1$, rather than $\alpha = 0$ —is shown in figures 1b and 1c. Overall better fit to the data is apparent, in particular, improvement in the transpiration rate during the first one-half of the life cycle. However, also clear is that even higher rates (in other words, higher α 's) are needed in the first one-third of the life cycle. Without fitting the data even further, we have nevertheless demonstrated the possibility of representing the transpiration to varying degrees of accuracy with formulations that have physical meaning.

CONCLUSION

Models such as these are the best way of examining the "interactions of assumptions" /9/. Considering the overall results, the logistic growth equations combined with the assumption that the rate of transpiration per unit inedible mass decreases during the life cycle of the crop will generally reproduce the data and will probably be adequate in highly aggregated models of a CELSS, for example, the BLSS model /1/. A physiological interpretation of this transpiration formulation and comparison of these findings to the transpiration formulations in more detailed models of non-hydroponic wheat /10,11/ (which, however, are presently not applicable to a CELSS model) will help the crop model shown here develop more complex dynamics and allow better preliminary designs of space agricultural systems.

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REFERENCES

1. J. D. Rummel and T. Volk, A Modular BLSS Simulation Model, *Adv. Space Res.*, 7, # 4, 59-67 (1987).
2. T. Volk, Modeling the growth dynamics of four candidate crops for controlled ecological life support systems, Final report to NASA/ASEE Summer Faculty Fellowship Program at Johnson Space Center, NGT44-001-800, 33-1 to 33-17 (1987).
3. T. Volk and H. Cullingford, Crop growth and associated life support for a lunar farm, *Lunar Bases and Space Activities of the 21st Century*, in press (1989).
4. S. Schwartzkopf, private communication (1987).
5. B. G. Bugbee and F. B. Salisbury, Studies on maximum yield of wheat for the controlled environments of space, in *Controlled Ecological Life Support Systems: CELSS '85 Workshop*, eds. R. D. MacElroy, N. V. Martello, and D. T. Smernoff, NASA-TM-88215, p. 447-486 (1986).
6. B. G. Bugbee, private communication (1988).
7. D. M. Gates, *Biophysical Ecology*, Springer-Verlag, New York (1980).
8. B. G. Bugbee, private communication (1986).
9. J. F. Reynolds and B. Acock, Modeling approaches for evaluating vegetation responses to carbon dioxide concentration, eds. B. R. Strain and J. D. Cure, *Direct Effects of Increasing Carbon Dioxide on Vegetation*, DOE/ER-0238, U. S. Dept. of Energy, Wash., D. C., p. 33-51 (1985).

10. T. Hodges and E. T. Kanemasu, Modeling daily dry matter production of winter wheat, *Agronomy Journal*, 69, 974-978 (1977).
11. S. J. Maas and G. F. Arkin, TAMW: A wheat growth and development simulation model, (Research Center Program and Model Documentation. No. 78-1), Blackland Research Center at Temple, Texas Agriculture Experiment Station, College Station, Texas (1980).

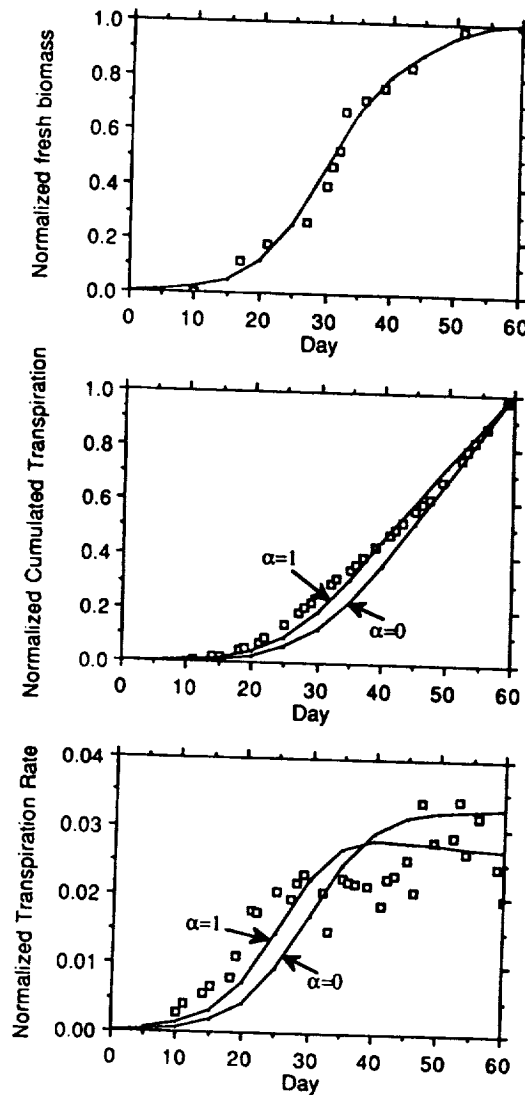


Fig. 1. Model results (lines) and empirical data (points) of (a, top) fresh biomass, (b, middle) cumulated transpiration, and (c, bottom) transpiration rate, all normalized as described in the text. Results in (b) and (c) are shown for two values of α ; α controls the time-dependence of the age factor f_a in the transpiration rate. When $\alpha = 0$, f_a is constant; when $\alpha = 1$, f_a decreases nonlinearly from about 2 in early growth to about 1 in late growth (see text). Results for biomass in (a) do not vary as a function of α . See equations 6a-b for definition of the normalized cumulated transpiration and normalized transpiration rate.